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COMPOSITION AND DYNAMICS OF THE SEED BANK OF COASTAL SCRUB IN BAJA CALIFORNIA

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ABSTRACT

Seed bank dynamics are a critical consideration for management of arid and semi-arid shrublands. In the threatened "coastal succulent scrub" vegetation (at Punta Banda, Baja California), we studied the seed bank's composition and size, as well as its dynamics as shown by field emergence and as inferred from literature reports on germination. We also analyzed sampling effort for both seeds and seedlings. The seed bank was sampled just prior to the rainy season, with 130 soil units of 7-cm diameter × 1-cm depth distributed systematically over 1.66 ha. The field samples were mixed together then laboratory samples (17 of 14 cm^3) were taken for manual extraction of seeds. We found 25 species, mostly of short-lived herbs. Some obvious species of the local flora were not encountered. Overall density was approximately 11,807 seeds m^{-2}, but densities differed by more than 100-fold among species. Analysis of sampling effort suggested that only 8–12 laboratory samples were needed to approach estimated asymptotes of the density of seeds and the number of species. Seedling emergence was recorded during four months on 30 randomly distributed and caged plots of 361 cm^2. We found 22 species, mostly short-lived herbs. Most species were uncommon and the density per plot of all species was highly skewed. Modes per plot were 3–4 species and 129–256 seedlings. Analysis of sampling effort suggested approximately 15 plots were needed to approach estimated asymptotes of the density of seedlings and the number of species. Published information on seed germination was found for 75 species which have been reported from coastal succulent scrub in the Punta Banda area. Apparently, fire-related cues were required for germination in only 13% of these, while most species may require only moist winters. However, long-term dynamics of the seed bank, and its geographic variation, remain to be studied.

RESUMEN

La dinámica del banco de semillas es un tema crucial para el manejo de matorrales de zonas áridas y semi-áridas. Estudiamos el tamaño y la composición del banco de semilla de matorral costero suculento en Punta Banda, Baja California. También observamos su dinámica, en la aparición de plántulas en el campo e inferida de reportes en la literatura sobre la germinación. Analizamos el efecto del esfuerzo de muestreo, ya que es el primer estudio del banco de semillas en matorral costero mediterraneo. El banco de semillas fue muestreado justo antes de la temporada de lluvias, con 130 unidades de 7 cm dia × 1 cm de profundidad y distribuidas sistematicamente sobre 1.66 ha. Las muestras de campo fueron mezcladas, luego se tomaron muestras de laboratorio (17 de 14 cm^3) para extraer las semillas manualmente. Encontramos 25 especies, principalmente de hierbas de corta vida; no se encontraron varias especies conspicuas de la vegetación local. La densidad general fue aproximadamente 11,807 semillas m^{-2}, pero entre las especies las densidades variaron por más de un factor de 100. Análisis del esfuerzo de muestreo sugirió que el número de especies y la densidad total de semillas fueron adecuadamente estimados con 8–12 muestras de laboratorio. La aparición de plántulas fue registrada durante cuatro meses en 30 cuadrantes enjaulados (de 361 cm^2) distribuidos aleatoriamente. Encontramos 22 especies, principalmente de hierbas de corta vida. En su mayoría, las especies fueron escasas y la densidad total por cuadrante fue altamente sesgada; se presentaron modas de 3–4 especies y 129–256 plántulas. El análisis del esfuerzo de muestreo sugirió un muestreo adecuado con 15 o más cuadrantes. Se encontró información publicada sobre la germinación de 75 especies que se encuentran en el matorral costero suculento del área de Punta Banda. Disparadores de la germinación relacionados con incendios fueron reportados, como obligatorios,

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en sólo el 13% de las especies. Aparentamente la mayoría de las especies germinan con cualquier invierno húmedo. No obstante, la dinámica a largo plazo de las especies y la biología de sus semillas, quedan por investigarse.

Key Words: coastal scrub, biodiversity, fire, germination, México, sampling, seed bank, vegetation dynamics.

Adequate management of mediterranean-climate shrublands requires an understanding of their diversity in the dimensions of physiognomy, floristics, environment, and dynamics. Among the features that distinguish California coastal scrub (Mooney 1977; Pase and Brown 1982; O'Leary 1990) from chaparral are the dominance of drought-deciduous shrubs (Harrison et al. 1971; Westman 1983), greater diversity of functional types across the geographic range of the vegetation (Peinado et al. 1994), and susceptibility to transformation from the combined effects of invasion and fire (Kirkpatrick and Hutchinson 1980; Minnich and Dezzani 1998). This vegetation is generally regarded as threatened or endangered in both Alta and Baja California due to increasing pressures of invasion and anthropogenic fire, together with urban development, agriculture and grazing (Westman 1981; O'Leary and Westman 1988; O'Leary 1990; Genin and Badán-Dangon 1991; Espejel 1993; Minnich and Dezzani 1998).

Nonetheless, information on the biology of the dynamics of California coastal scrub is scant, compared to the adjacent chaparral vegetation, and mostly refers to response to extreme stress (anthropogenic fire) in the Venturan and Riversidian associations in Alta California (reviewed in O'Leary 1990; see also DeSimone and Zedler 1999). In the chaparral, many species of shrubs and herbs are known to have large seed banks which can persist for many years, and to have germination improved by, or perhaps limited to, burned conditions (Sweeney 1956; Zammit and Zedler 1988, 1994; Parker and Kelly 1989; Keeley 1991). Of course, neither of these characteristics is universal among chaparral species, but they are sufficiently common that the dynamics of the vegetation is usually discussed in relation to a "fire cycle." For coastal scrub, we are unaware of direct data on community seed banks.

In coastal sage scrub, the continuous recruitment of shrubs and, apparently, of herbaceous perennials and some annuals suggest much of the system may be in flux in the absence of fire (Westman 1981; Malanson and O'Leary 1982; Keeley and Keeley 1984). Continuous regeneration is affected by disturbance of biotic origin and microlocal scale (DeSimone and Zedler 1999), and of course, "pyrophytes" are present at some sites. In the southern succulent variant of coastal scrub, the only study to date of regeneration was also initiated after a fire, but included all life forms and showed several modes of regeneration or life cycle strategies, including a few species that appeared to be fire dependent (Cruz 1997). However, there has been no attention to the structure and dynamics of seed banks that must figure in regeneration of coastal scrub, in any of its various forms or environments. This paper aims to contribute to the understanding of the dynamics of coastal succulent scrub through investigation at one site in Baja California. We studied the size and composition of the seed bank and seedling emergence in undisturbed conditions, and also compiled published information on the germination of species found at or near our site, based on horticulture, experimental studies and field observations (although in most cases the seed provenance or site was more than 100 km distant from our field site).

Of course, the study of organisms in soil involves inherently difficult problems of sampling. Although it was not our purpose to compare different sampling techniques, an evaluation of different sampling intensities was an important goal, for both the seed bank and *in situ* germination. In this context, we made some methodological innovations that may facilitate other studies (and their comparison), and also found some provocative results that beg further basic study and contribute to discussions of management.

METHODS

The study site was on the small peninsula of Punta Banda in the State of Baja California, México, at about 31°43′48″N, 116°43′12″W and ca. 100 m elevation (Fig. 1). In the context of broad geographic variation in coastal scrub, our site was in the coastal succulent scrub formation and the Martirian association of Westman (1983). It was intermediate between the Diegan coastal sage scrub and Martirian coastal succulent scrub of Zippin and Vanderweir (1994), and corresponded roughly to the *Bergerocactus emoryi–Agave shawii* association of Peinado et al. (1995) although *B. emoryi* was rare. The site does not correspond well to any of the California floristic series in Sawyer and Keeler-Wolf (1995). The most common perennials at our sample points were *Eriogonum fasciculatum, Agave shawii, Viguiera laciniata, Artemisia californica, Simmondsia chinensis,* and *Dudleya* spp.; less common species were *Euphorbia misera, Lotus scoparius, Rhus integrifolia, Mammillaria dioica,* and species of *Hazardia* and *Isocoma*; rare perennials included *B. emoryi, Salvia munzii, Ferocactus viridescens,* and *Cneoridium dumosum.* Grasses were noted at less than 11% of the points. Sampling of our site and others in the same association on Punta Banda was also done by Espejel (personal

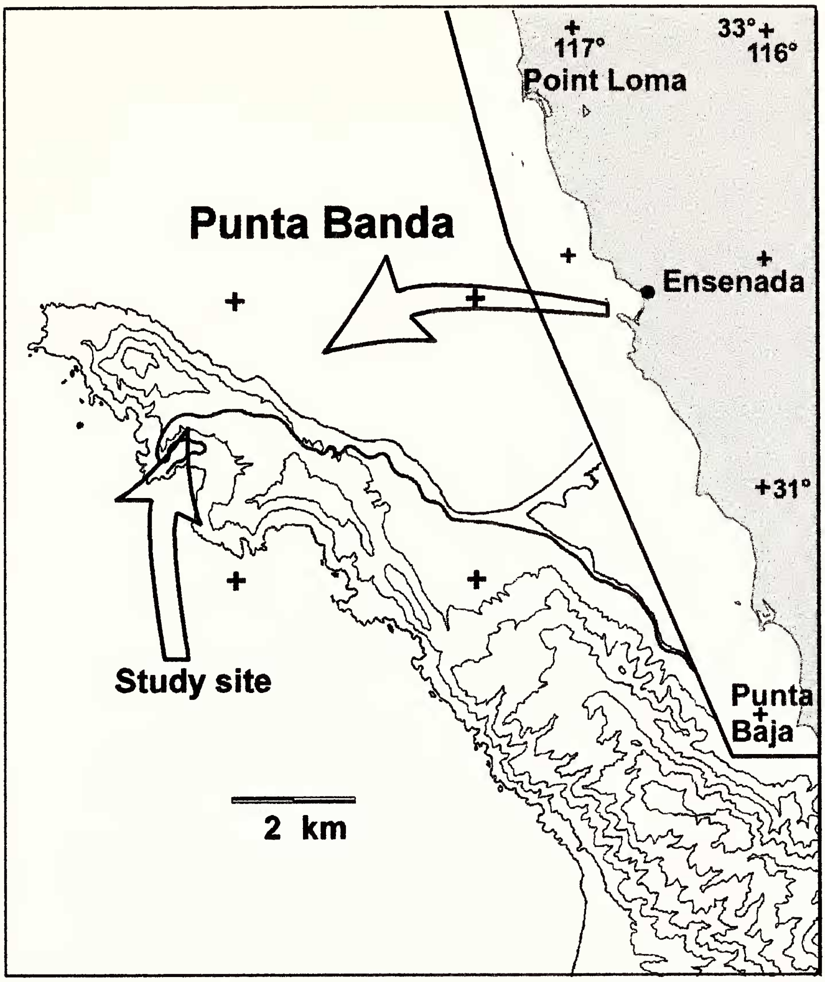

FIG. 1. Maps of Punta Banda, showing location of the study site, and of the region with Diegan and Martirian coastal scrub, showing the location of Punta Banda.

communication). A floristic list for Punta Banda (covering >3000 ha and including other vegetation types) was published by Mulroy et al. (1979). Nomenclature here follows Hickman (1993).

We chose our site from among accessible south-facing slopes, without appreciable ravines or ridges over at least one hectare, and within the largest patch of well-preserved vegetation. The topographic conditions probably supported a less-diverse flora than might be found on more rugged or moister areas of the point. There were no signs of trails, roads or former structures, and only scant and aged signs of livestock and some exotic flora. There were no signs of recent fire, and mapping from aerial photographs suggested no fires in at least 40 yr (R. Minnich personal communication). Rocks of porfirite and andesite littered much of the site. Soil analysis showed moderately acid conditions (pH 5.57 ± 0.4 [SD]; n = 9) with variable organic carbon (1.85–6.23%), a clay fraction of 29.19 ±1.92% and a sand fraction of 32.97 ±2.75%. Climatic data were available for Ensenada, ca. 17 km NNE of the site. There, annual precipitation averaged 271 mm (range 102–612, for 68 yr between 1894 and 1998), and monthly mean temperatures ranged from 7 to 14°C.

Field soil samples were taken at the end of October 1993, before the first winter rains, on a plot of 104 m by 160 m at alternate points on an 8 m grid, so there were 130 samples. Each sample was 7 cm in diameter and 1 cm deep (or less in the presence of rocks). After removal of rocks, sticks, leaves, roots, *Selaginella* and feces, the field samples were thoroughly mixed together using a gem-grinding drum. The bulk lot amounted to 3.370 liters and 4.744 kg. Laboratory samples of 14 cm^3 were taken from this bulk lot, and propagules were separated with dissecting needles under a microscope. Species were identified from reference collections and with the assistance of a specialist. Emergence of seedlings was observed in the field between January and May (1994), in 30 plots of

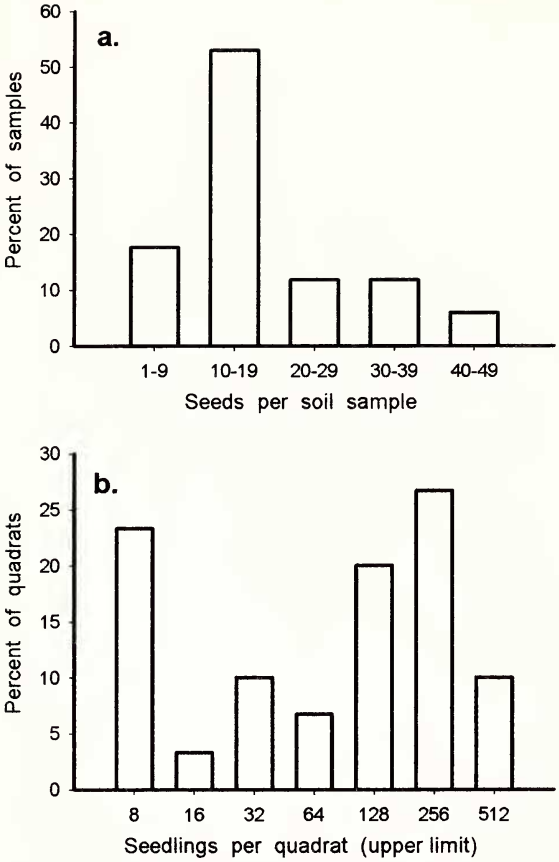

FIG. 2. Frequency distributions of a) number of seeds per aliquot of the mixed soil sample, and b) number of seedlings per quadrat.

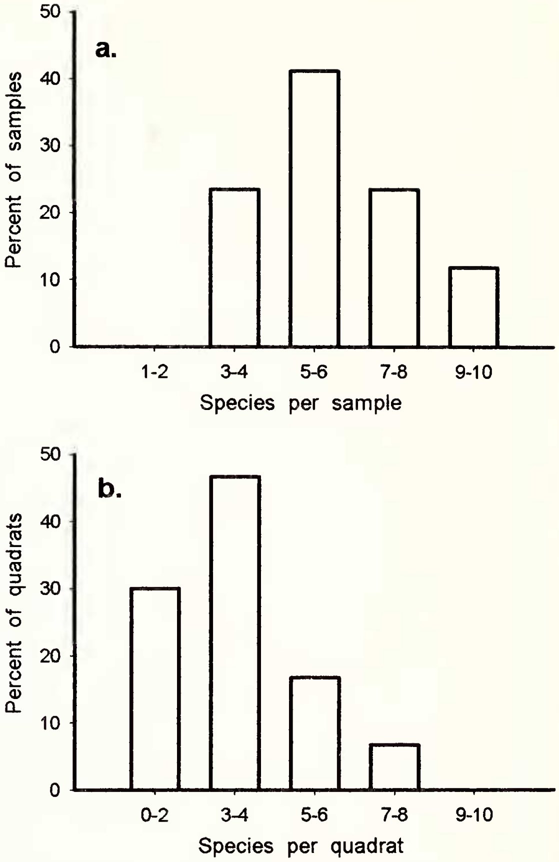

FIG. 3. Frequency distributions of a) number of species of seeds per aliquot of the mixed soil sample, and b) number of species of seedlings per quadrat.

19 cm by 19 cm, distributed at random over the same area from which the soil was sampled, with each plot protected by a hard wire cage, 5 cm high with 1 cm mesh. Unfortunately, due to technical problems it was not possible to identify all seed or seedling species.

The effect of cumulative number of samples on cumulative number of species and total species richness, were examined for both the seed bank and seedling data using the EstimateS software of Colwell (2000). Indices reported and discussed here are the S_{obs}, Jack 1 and Chao 2. The ICE index is not presented here for three reasons: its definition changes at 10 samples; its error goes to zero as cumulative number of samples approaches the maximum; and its behavior with our data was not close to a monotonic increase. For each index and data set, 50 randomizations of sample order were examined, without replacement.

RESULTS

Seeds in Soil

A total of 17 laboratory samples of soil were examined, yielding 281 seeds of 25 species. The number of seeds per sample was not normally distributed despite prior mixing, but there were no samples without seeds (Fig. 2a). The modal category was 10–19 seeds. The number of species per sample ranged from three to nine with a mode of 5–6 (Fig. 3a). Nine morphospecies could not be identified to family and five others were identified only to family level. We encountered seeds of two cactus species, as well as four Asteraceae and three Poaceae, probably all natives. The only dominant shrub encountered was *Eriogonum fasciculatum.*

Almost two-thirds of the species were represented by a total of less than four seeds in the 17 samples (Fig. 4a). The most abundant seeds were of *Crassula connata* (49% of the total), *Hemizonia* sp. (14%) and *E. fasciculatum* (9%). Notably, sporocarps of *Selaginella* species were almost as abundant as *C. connata* seeds. Seed size among the species encountered ranged from 0.25 to 2.8 mm in the longest dimension.

Seedlings

In the 30 protected plots, we recorded a total of 3148 seedlings of 22 species. The range was zero

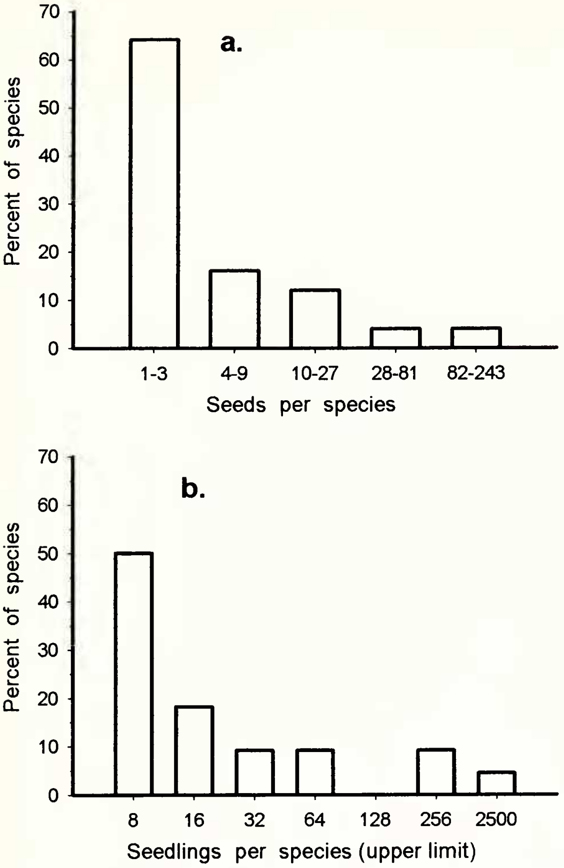

FIG. 4. Frequency distributions of a) total number of seeds per species in all aliquots of the mixed soil sample, and b) total number of seedlings per species in all quadrats.

to 512 seedlings per plot and the distribution was extremely skewed (Fig. 2b). More than a third of the plots contained fewer than 64 seedlings, but about a third of all the seedlings occurred in just 10% of the plots. The number of species per plot ranged from zero to seven, with a mode of 3–4 (Fig. 3b). Three morphospecies, represented by a total of 11 seedlings, were not identified to family, and seven were identified only to genus. The family with the most species was Asteraceae (six), followed by Poaceae and Polemoniaceae (three each), Crassulaceae and Scrophulariaceae (two), and Brassicaceae, Fabaceae and Valerianaceae (one). Only two of the identified species were perennials (*Festuca* sp. and *Dudleya lanceolata*), and only one was clearly not native (*Sonchus oleraceus*).

More than 68% of the species were represented by a total of less than 17 seedlings in the 30 plots (Fig. 4b). On the other hand, the most abundant species was *C. connata* that accounted for 78% of all seedlings and occurred in 63% of the plots. The next most abundant species were *Navarretia atractyloides* and *Festuca* sp., accounting for an additional 14% of all seedlings. The exotic *S. oleraceus* accounted for 0.3% of all seedlings and occurred in 17% of the plots.

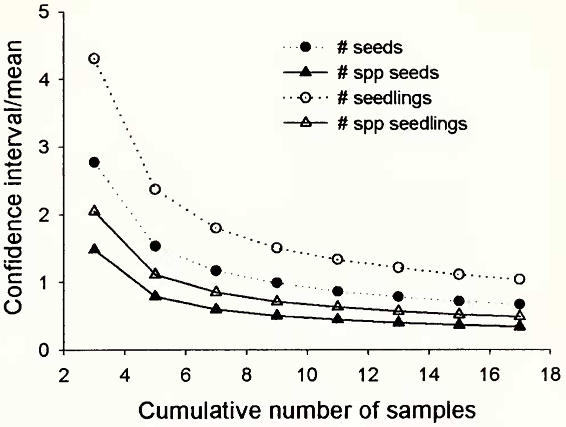

FIG. 5. Effect of cumulative sample size on the ratio of confidence interval to mean (bootstrapped trends).

Sample Size

To examine the effect of the number of samples on estimates of the mean number of individuals and of species per sample unit for both the seed bank and seedlings, confidence intervals were estimated for a range ($\geq$3) of cumulative number of samples, using bootstrap techniques. The ratio of confidence intervals to means showed a smooth progression in all cases (Fig. 5): ratios were larger for number of individuals than for number of species, although means were much larger for individuals, and ratios were larger for seedlings than for seeds. The decline of the ratios appeared to be asymptotic.

The effect of cumulative number of samples on estimates of accumulated and total number of species of seeds and seedlings was examined with three indices (Fig. 6). S_{obs} showed the slowest rise in cumulative number of species; this index was not asymptotic but necessarily reached the total numbers of species observed at the full sample sizes for seeds and seedlings. Jack 1 started at similar values to S_{obs} but rose more quickly and to higher values. It reached an asymptote of about 30 species at about 12 samples for the seed bank; for seedlings, Jack 1 showed most species were found within 19 quadrats, but the curve continued to increase slowly even above 27 species in 25 quadrats. Compared to Jack 1, the Chao 2 index estimated more species at a smaller cumulative number of samples but the asymptotes were lower; it also reached asymptotes sooner, at about 8 samples for seeds and about 14 for seedlings. Chao 2 estimated that there should be a total of about 26 species in both cases, which was an interesting coincidence given the independent sampling of seeds and seedlings.

TABLE 1. EVIDENCE FOR HEAT EFFECT ON GERMINATION OF COASTAL SUCCULENT SCRUB SPECIES. The floristic list for Punta Banda derives from Mulroy et al. (1979) and Espejel (personal communication). Germination information is for seeds from other provenances in horticultural treatment or experiments, reported by 1) Emery (1988) and 2) Keeley (1991), or from field observations by 3) DeSimone and Zedler (1999) and 4) this study. Symbols: -, germination without a fire-related stimulus; +, germination with fire-related stimulus or alternative seed-coat softening factors; ±, mixed or conflicting results.

Family	Species	Heat effect	Sources
Liliaceae	*Agave shawii*	–	1
	Allium praecox	–	2
	Calochortus splendens	–	1, 2
	Dichelostemma capitatum	–	1, 2
	Zygadenus fremontii	–	1, 2
Poaceae	*Achnatherum coronatum*	–	1, 2
	Muhlenbergia microsperma	–	4
	Nassella cernua	–	1
	Nasella pulchra	–	1, 2
	Poa secunda	–	1
	Vulpia octoflora	–	4
Anacardiaceae	*Malosma laurina*	+	1, 2
	Rhus integrifolia	+	1, 2
Asteraceae	*Artemisia californica*	±	2, 3
	Coreopsis maritima	–	1
	Encelia californica	–	1, 2
	Gnaphalium bicolor	–	1
	Gnaphalium californicum	±	2, 4
	Hazardia orcuttii	–	1
	Ericameria palmeri	–	1
	Isocoma menziesii	–	1, 2
	Heterotheca grandiflora	–	2
	Filago arizonica	–	4
	Lasthenia californica	–	4
	Porophyllum gracile	–	1
	Rafinesquia californica	+	2
	Trixis californica	–	1
Boraginaceae	*Cryptantha intermedia*	+	2
Brassicaceae	*Descurainia pinnata*	–	2
	Lepidium nitidum	±	2, 4
	Streptanthus heterophyllus	+	2
Cactaceae	*Ferocactus viridescens*	–	1
Capparidaceae	*Cleome isomeris*	–	1
Caryophyllaceae	*Cardionema ramosissimum*	–	1
	Spergularia macrotheca	–	1
Chenopodiaceae	*Atriplex canescens*	–	1
Convolvulaceae	*Calystegia macrostegia*	±	1, 2
Crassulaceae	*Crassula connata*	–	4
	Dudleya lanceolata	–	1, 4
Cucurbitaceae	*Marah macrocarpus*	–	1, 2
Euphorbiaceae	*Acalypha californica*	–	1
	Chamaesyce polycarpa	–	1
Hippocastanaceae	*Aesculus parryi*	–	1
Hydrophyllaceae	*Emmenanthe penduliflora*	+	1, 2
	Phacelia cicutaria	±	1, 2
	Phacelia parryi	+	2
Fabaceae	*Lotus strigosus*	+	1, 2
	Lotus hamatus	+	1
	Lotus salsuginosus	+	2
	Lotus scoparius	±	1, 4
	Lupinus bicolor	+	1
	Lupinus hirustissimus	+	1
	Lupinus longifolius	+	1
	Lupinus sparsiflorus	+	1
	Lupinus trancatus	+	1
Lamiaceae	*Salvia apiana*	±	1, 2, 3
Malvaceae	*Malacothamnus fasciculatus*	+	2
Nyctaginaceae	*Mirabilis californica*	–	1
Onagraceae	*Clarkia epilobioides*	+	2

TABLE 1. CONTINUED.

Family	Species	Heat effect	Sources
Polemoniaceae	*Linanthus* sp.	−	4
	Navarretia atractyloides	−	4
	Navarretia sp.	−	4
Polygonaceae	*Eriogonum fasciculatum*	−	1, 2, 3
	Eriogonum grande	−	1
Portulacaceae	*Claytonia perfoliata*	−	1
Primulaceae	*Dodecatheon clevelandii*	−	1
Rubiaceae	*Galium angustifolium*	+	2
Rutaceae	*Cneoridium dumosum*	−	1, 2
Scrophulariaceae	*Antirrhinum kelloggii*	−	4
	Castilleja exserta	−	1
	Castilleja foliolosa	−	1
	Linearia canadensis	−	4
	Mimulus aurantiacus	−	1, 2
Simmondsiaceae	*Simmondsia chinesis*	−	1
Valerianaceae	*Plectritis* cf. *ciliosa*	−	4

Germination

Reports concerning conditions for seed germination have been found for 75 species of the flora of Punta Banda coastal scrub. Table 1 summarizes this information with regard to whether seeds may commonly germinate with only climatically-typical conditions of moisture and temperature. The particular concern is whether heat or some fire-related factor is necessary for germination. The information is based in part on experimental studies of germination in species that occur in chaparral (Keeley 1991), and in part on horticultural experience and experiments (Emery 1988). Additional information came from our and others' recent field observations (Cruz 1997; DeSimone and Zedler 1999).

According to our review, about 75% of the species in our extended-local flora will germinate without a fire-related stimulus (− in Table 1). The literature suggests that some species have multiple mechanisms for germination, e.g., softening of the seed coat is an alternative to fire-related factors (+ in Table 1); however, the natural history interpretation remains obscure. There are also some taxa that have given either mixed or conflicting results (± in Table 1; see also Keeley 1986).

DISCUSSION

Overall, the seed bank was not impressively large for the available space or in comparison with chaparral (Zammit and Zedler 1988) or with North American warm deserts (Kemp 1989). Our data suggest an overall density of only 1.2 seeds cm^{-2}, or about 11,807 seeds m^{-2}, and about 26–30 species. Also, the abundance of seeds varied among species by more than two orders of magnitude, so that most species were quite rare. The great variation among sympatric species and among habitats in mediterranean climate areas has been emphasized by other authors (Parker and Kelly 1989, Zammit and Zedler 1994). Apparently, the present study is the first in any type of coastal scrub in the California bioregion; as such, the field results should not be considered representative of coastal scrub.

The seed bank, seedling and annual vegetation, and mature perennial vegetation differed strikingly in composition, with perhaps two exceptions. Both the seed bank and seedling vegetation were largely dominated by *Crassula connata,* a diminutive annual succulent with very small seeds, and other annual herbaceous species. We did not encounter seeds of most species that were prominent in the vegetation (e.g., *Euphorbia misera,* which has explosive fruits, and *Artemisia californica*). One hypothesis might be that their seeds are short-lived and are not produced in abundance every year. The absence of seeds of some common perennials such as *Simmondsia chinensis, Agave shawii* and *Rhus integrifolia,* might reflect infrequent seed production, or might represent a relatively low reproductive output that is concentrated in larger and fewer propagules, which are correspondingly rarer. Larger seeds may also be more susceptible to predation. In contrast, *Eriogonum fasciculatum,* a common shrub with seeds roughly 1.5–2 orders of magnitude smaller in volume than the above species, was apparent in the seed bank but absent among the seedlings. Altogether, this relatively uniform and stressful site showed a small flora below ground as well as above.

Sampling of seed banks is generally neglected because of its inherent difficulties. Our procedure may allow a site-level rapid assessment: we collected only 0.003% of the site surface, and examined only 4.8% of that collection, but we estimated that species number was asymptotic species numbers after about 59% of that sample. Undoubtedly species were missed with this procedure, as with any other, and sampling at one or two orders of magnitude greater intensity would reveal species that are rare in the seed bank (whether common or

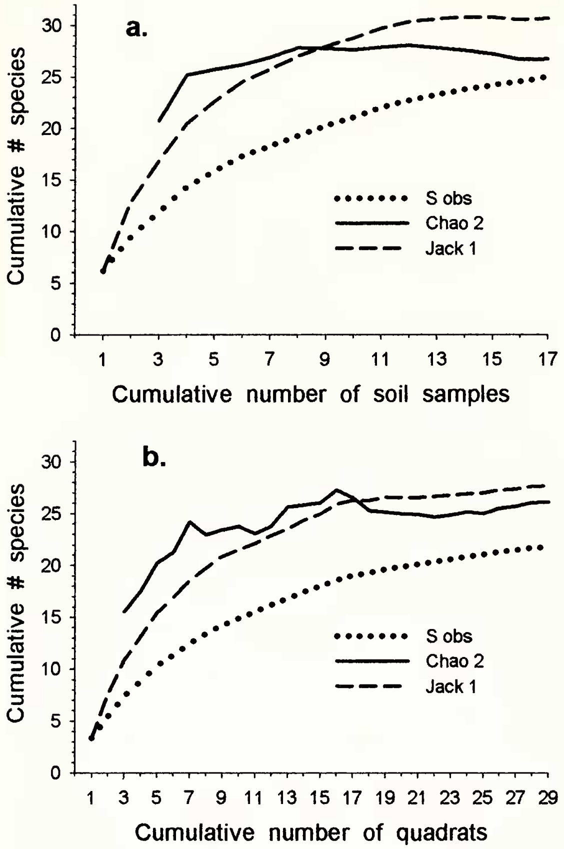

FIG. 6. Effect of cumulative sample size on indices of cumulative number of species of a) seeds and b) seedlings.

rare in the vegetation). Nonetheless, we suggest that eliminating spatial variability from the seed bank provides a useful simplification for survey and comparative studies of species number, composition and seed density, particularly for herbaceous species. The seedling data suggest that seed distribution is heterogeneous and not "normal," so bulking the field samples should improve the chances of finding less common species, and provide a site-level estimate of density. Of course, sites with greater variation in cover, drainage, slope and exposure may require a greater intensity or different structure of sampling and analysis.

The depth of our sampling may be a concern, particularly if the seed rain differs much across years, or if seed predators are selective of species that may slowly build a large seed bank due to multi-year dormancy. Moreover it would be useful to investigate whether species in the near-surface seed bank, which is susceptible to erosion and to destruction in fires, are also at greater depth. However, a sampling protocol with a greater fixed depth would have required much rock chiseling and/or crevasse cleaning in our case, and a protocol of variable depth creates problems with extrapolation to surface area.

The estimate of the total number of species in a community depends to some extent on the choice of statistical procedure. The simple and infrequently-used bootstrap procedure (S_{obs}) suggested sampling was not adequate for either seeds or seedlings. In contrast, the more widely-used procedures of Jack 1 and Chao 2 suggested our sample size was more than adequate for seeds and adequate for the seedling community. However, these two procedures differed substantially in estimates for the asymptotic number of species of seedlings, a result which was probably due to the non-uniform distributions of species and seedlings.

Although recent invasions and changes in land-use and culture will probably make fire an increasingly prominent factor (Keeley 1982; Minnich 1983; Minnich and Dezzani 1998; Keeley and Fotheringham 2001), the great majority (ca. 75%) of the species of coastal succulent scrub at Punta Banda probably germinate without a fire-related stimulus. Moreover, the list is certainly an underestimate and could reasonably be augmented with other species based on the consistency of these characters with respect to taxonomy and life form (e.g., most Asteraceae, Cactaceae, Poaceae, *Dudleya, Allium, Jepsonia*). What fraction of the seed bank is actually dormant remains to be determined. Field germination might have amounted to ca. 25% of the seed bank in our case, based on an estimate of 2907 seedlings m^{-2} (although this is based on a very non-normal distribution). A particularly curious case was the absence of *E. fasciculatum* from the seedlings, despite its present in the seed bank.

The reports on germination requirements of some species show mixed or conflicting results, which suggest that either germination occurs to some extent without fire but is augmented by fire (e.g., Stone and Juhren 1951, 1953), or that seed age and condition may be complicating factors (Odion 2000), or that geographic variation may be significant. Most of the information in Table 1 derives from seeds from localities other than our study site, although this is standard usage. Remarkably, geographic (and particularly historical) variation in germination characteristics has been ignored in shrubland species of the Californian bioregion, with rare exception (e.g., Capon and Brecht 1970; Keeley 1986). Variations within plants or with populations have fared only slightly better (Cook et al. 1971; Zammit and Zedler 1988, 1994). Unfortunately, despite the interest of Baja California as a biological and climatic transition zone (Shreve 1936; Bullock 1999), we know of no studies on germination from Baja California populations in coastal scrub or chaparral. Some species which are supposed to have large and persistent seed banks elsewhere, were not apparent in the seed bank at our site despite presence (if not abundance) of the plants. This may be another indication that seed biology is not necessarily homogeneous, although it would be premature to speculate about specific factors.

Apparently, the seed bank is a limited asset for conservation management in the face of pastoral-agriculture uses and suburban-urban development. For the restoration of disturbed or denuded sites, movement of soils would not be efficient for establishing vegetation structure but might have some interest for introduction of the herbaceous flora. Also, the superficial seed bank we studied might be largely lost in severe fires or with the typical pre-construction razing of the surface. Fire, overwhelmingly anthropogenic, is a dramatic and powerful force in reorganizing coastal scrub in general (O'Leary 1990; Cruz 1997). The weight of evidence suggests an appreciable element of the coastal succulent scrub in our area is dependent on fires for germination, but the vast majority of species are not. In an average winter, germination was abundant but showed mostly annual species, in terms of numbers of individuals and of species. Moreover, most of the dominant shrubs did not form large, dormant seed banks, unlike the common conception of some major species of the chaparral (Parker and Kelly 1989). The broader-scale, longer-term and contingent behavior of the seed bank remains to be studied, but we hope this initial exploration may serve to provoke and even instruct further study.

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